Biological Conservation 248 (2020) 108678

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Preserving connectivity under climate and land-use change: No one-size-fits-all approach for focal species in similar habitats

Jennifer K. Costanza[a,*], James Watling[b], Ron Sutherland[c], Curtis Belyea[d], Bistra Dilkina[e], Heather Cayton[f], David Bucklin[g], Stephanie S. Romañach[h], Nick M. Haddad[f]

[a] Department of Forestry and Environmental Resources, North Carolina State University, Research Triangle Park, NC, USA
[b] Department of Biology, John Carroll University, University Heights, OH, USA
[c] Wildlands Network, Durham, NC, USA
[d] Biodiversity and Spatial Information Center, Department of Applied Ecology, North Carolina State University, Raleigh, NC, USA
[e] Department of Computer Science, University of Southern California, Los Angeles, CA, USA
[f] Kellogg Biological Station and Department of Integrative Biology, Michigan State University, Hickory Corners, MI, USA
[g] Fort Lauderdale Research and Education Center, University of Florida, Fort Lauderdale, FL, USA
[h] U.S. Geological Survey, Wetland and Aquatic Research Center, Fort Lauderdale, FL, USA

ARTICLE INFO

Keywords:
Climate adaptation
Climate refugia
Corridor
Land-use change
Landscape conservation
Protection status

ABSTRACT

Habitat connectivity is essential for maintaining populations of wildlife species, especially as climate changes. Knowledge about the fate of existing habitat networks in a changing climate and in light of land-use change is critical for determining which types of conservation actions must be taken to maintain those networks. However, information is lacking about how multiple focal species that use similar habitats overlap in the degree and geographic patterns of threats to linkages among currently suitable habitat patches. We sought to address that gap. We assessed climate change threat to existing linkages in the southeastern United States for three wildlife species that use similar habitats but differ in the degree to which their ranges are limited by climate, habitat specificity, and dispersal ability. Linkages for the specialist species (timber rattlesnake), whose range is climate-restricted, were more likely to serve as climate change refugia – that is, they were more likely to be climate-stable – by the middle of the 21st century. This contrasts with the two more generalist species (Rafinesque's big-eared bat and American black bear), whose linkages were threatened by climate change and thus required adaptation measures. Further incorporation of projected land-use change and current protection status for important linkages narrows down our recommended conservation actions for each species. Our results highlight the surprising ways in which even species that use similar habitats will experience differences in the degree and geographic patterns of threats to connectivity. Taking action before these projected changes occur will be critical for successful conservation.

1. Introduction

The long-term viability of populations often depends on regional habitat connectivity (Costanza and Terando, 2019; Heller and Zavaleta, 2009; Littlefield et al., 2019; UNEP, 2019). A network of connected habitat can support large, genetically-diverse populations that enhance the capacity of species to adapt to a changing climate (Rudnick et al., 2012). Likewise, connected habitat increases the likelihood that species can track suitable areas in a changing climate (McGuire et al., 2016; Nuñez et al., 2013). A variety of connectivity approaches that have the specific aim of climate change adaptation are becoming popular (for example, see the typology of approaches in Keeley et al., 2018). One set of approaches focuses on facilitating movement in response to climate change by identifying linkages in the form of corridors, least-cost paths, stepping stones, or other landscape features connecting existing habitat cores with habitat that is projected to be suitable at some point in the future (Keeley et al., 2018; Lawler et al., 2013). However, missing in those approaches, and crucial for efforts that focus on conserving species within their current ranges, is an assessment of how existing linkages among currently suitable habitat patches for focal species will be affected by a changing climate, and the degree to which those linkages remain suitable over time (Keeley et al., 2018).

Within a species' current range, existing linkages might be climate-stable compared to the rest of the landscape – so-called climate change

* Corresponding author at: 3041 Cornwallis Rd., Research Triangle Park, NC 27709, USA.
E-mail address: jennifer_costanza@ncsu.edu (J.K. Costanza).

https://doi.org/10.1016/j.biocon.2020.108678
Received 18 November 2019; Received in revised form 10 April 2020; Accepted 17 June 2020
Available online 10 July 2020

refugia (Keppel et al., 2012; Morelli et al., 2016) – or they may be highly threatened by climate change. The degree of climate change threat to a linkage can inform the priority conservation actions for that linkage: maintenance and enhancement of existing connectivity in linkages that are refugia, versus adaptation measures such as assisted migration or alternative linkages where threat is high (Hällfors et al., 2017; McLachlan et al., 2007). Thus, knowing which linkages are more likely to be refugia for a given species is critical to determine conservation actions. Ecological theory predicts that climate refugia may be more likely to occur in mountainous areas, where the future rate of climate change (termed climate change "velocity", Loarie et al., 2009) is likely to be low (Morelli et al., 2016). While literature points to these general characteristics of refugia, no study has evaluated whether multiple species that use similar habitats are likely to experience spatial overlap in the location of linkages that are refugia.

Furthermore, species, populations, and their habitat can experience synergistic negative effects from interactions between land-use change and climate change, which influence the appropriate conservation actions (Mantyka-Pringle et al., 2012, 2016; Oliver et al., 2012). For example, where land-use change threat is also high, climate adaptation measures may be restricted to ex-situ strategies like managed relocation to sites with lower threats. Investigating how appropriate actions can vary across connectivity networks with both land-use and climate change in mind will be critical for effective connectivity conservation.

We evaluate whether existing linkages in the form of least-cost paths among habitat cores may become climate change refugia for multiple focal species, and examine the priority conservation and adaptation measures that may be needed for each species as a result of likely future climate and land-use change. We focus on the southeastern United States (U.S.; "the Southeast"), which is an ideal region within which to examine climate threats and refugia. The Southeast spans several ecoregions (Fig. S1) and thus covers areas where climate change velocity is expected to be high (coastal plains) and low (mountains). Linkages among existing habitat patches may be particularly important to allow species to track changes in climate in the region (McGuire et al., 2016). In addition, the Southeast as a whole is projected to undergo substantial urbanization by the middle of the 21st century, particularly in the central portion of the Piedmont ecoregion (Terando et al., 2014; see Fig. S1 for ecoregion map), which could highly impact connectivity.

We present a case study that identifies climate and land-use change threats to existing habitat linkages for three vertebrate animal species that use similar habitats but exhibit a range of life histories and behaviors in the Southeast: timber rattlesnake (*Crotalus horridus*), Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), and American black bear (*Ursus americanus americanus*). These species differ in their home range sizes and dispersal abilities, but all use bottomland hardwood forests in the Southeast (NatureServe, 2019). All three are of conservation concern in at least portions of their range (NatureServe, 2019), yet they differ in the extent to which their geographic ranges are limited by climate in the region. For each of the three focal species, we identified and mapped linkages based on recent climate and land-use conditions and evaluated the likely threat to the linkage networks as a result of climate change by 2050. We then evaluated the degree of projected land-use change and protection status for the most important linkages in each species' habitat network.

We aimed to address these questions:

1. How does the degree of threat to connectivity from climate change compare for species that use similar habitat but vary in their life history characteristics?
2. How do the geographic patterns of climate change threat to existing habitat linkages vary among these species?
3. Do the linkages within the mountain ecoregions tend to be refugia, retaining relatively high suitability over time, compared to other ecoregions?
4. How do the types and geographic patterns of priority conservation actions needed for maintenance or adaptation in each species' habitat network compare among species?

2. Methods

2.1. Study area and focal species

The study area spans the Southeast U.S. and includes a series of adjacent ecoregions running from the coastal plain to the Piedmont to the mountains (Environmental Protection Agency (EPA), 2004; Fig. S1). This region encompasses both latitudinal and elevational gradients (Fig. S2) and therefore a range of biophysical conditions across which to evaluate conservation in the context of climate change. Average annual temperatures across the Southeast are likely to increase by as much as 2.4 °C by the middle of the 21st century, including increases in every season (USGCRP, 2017). Precipitation changes are more uncertain, but include the possibility of increased winter precipitation in the northern parts of the region, and decreased summer precipitation in the southern portion of the region (USGCRP, 2017). In addition, urban land use is expected to at least double its current extent in the region by the middle of the 21st century, with formation of a "Southern Megalopolis" of connected urban land use projected in the Piedmont (Terando et al., 2014).

To select focal species and map their existing connectivity networks, we worked iteratively with a team of conservation biologists and natural resource managers from the Landscape Conservation Cooperative (LCC) partnerships in the region. These LCCs are now part of the Southeast Conservation Adaptation Strategy (SECAS; http://secassoutheast.org/), a partnership among public and private organizations that is focused on cross-jurisdictional conservation planning and design.

We identified three species as targets for this work: Rafinesque's big-eared bat, the American black bear, and the timber rattlesnake. The American black bear is the most generalist of the three species, preferring mesic forest habitats, but also making extensive use of a variety of forest, swamp, agricultural lands and human-dominated habitats throughout its large geographic range (Stratman et al., 2001). The species is able to disperse relatively long distances and its reported home range size averages 26 km^2 (Table S1, Lee and Vaughan, 2003). The Rafinesque's big-eared bat is a southeastern endemic species that makes extensive use of bottomland hardwood forest for foraging and roosting. It also uses upland habitats to a lesser degree, and roosts in structures such as abandoned buildings and mines (Johnson, 2012; Johnson et al., 2012; Johnson and Lacki, 2013). The average reported home range size of the Rafinesque's big-eared bat is an order of magnitude smaller than the American black bear at 1.4 km^2 (Table S1). The timber rattlesnake occurs throughout the eastern and central U.S. and is often associated with bottomland hardwood forest in the Southeast (Steen et al., 2007), but will also use pine savanna, upland hardwood and mixed pine-hardwood forests, and agricultural fields (Waldron et al., 2006a,b). Its reported home range size is an order of magnitude smaller than the bat at 0.2 km^2 (Table S1).

The Rafinesque's big-eared bat and timber rattlesnake are listed as species of greatest conservation need in several states in the Southeast (NatureServe, 2019) because their populations are declining and are particularly affected by habitat loss and fragmentation (Bayless et al., 2011; Clark et al., 2010). Populations of the American black bear in the Southeast have been relatively stable recently but the species is of conservation focus in the Southeast, and habitat connectivity is of particular need because the species relies on large sparsely-settled blocks of habitat which are disappearing rapidly in the region (Larkin et al., 2004). The three species differ in the extent to which their ranges are limited by climate in the Southeast, with the timber rattlesnake being most sensitive to climate gradients in the region (Lawing and Polly, 2011).

2.2. Modeling and mapping connectivity networks

For each of the three focal species, we mapped the existing connectivity network as a set of habitat cores and least-cost linkages among them. To identify cores and linkages, we began by building an ecological niche model (ENM; Peterson et al., 2011) for each species. In each ENM, the habitat suitability across the entire study area for a species was predicted based on the relationship between observed occurrence points for a single species and environmental variables. We obtained geographic coordinates of species observations directly from species experts at state wildlife agencies or state heritage programs, online databases, and primary literature. Natural resource managers and biologists involved with SECAS helped us compile data, identify known places in each species' geographic distribution that were not represented by the initial data, contact individuals or consult additional resources to fill observed gaps in the point data, and re-evaluate the result. In the end, we used 619 points to construct ENMs for the Rafinesque's big-eared bat, 1458 points for the timber rattlesnake, and 7607 points for the American black bear. Environmental variables that were inputs to the ENMs included rasters of land cover (from the National Land Cover Dataset, 2006 version, Wickham et al., 2014) and seven bioclimate variables (annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, annual temperature range, total annual precipitation, total precipitation of the wettest month, and total precipitation of the driest month) obtained from 1971 to 2000 normals from the Worldclim dataset with a spatial resolution of 30 s (approximately 1 km^2 grid cells) (Hijmans et al., 2005).

To maximize ENM model performance (Hao et al., 2019), we used an ensemble modeling approach in which predictions from five algorithms (generalized linear models (McCullagh, 1984); multivariate adaptive regression splines (Friedman, 1991); generalized boosting models (Elith et al., 2008); random forests (Breiman, 2001); and maximum entropy (Phillips et al., 2006)) were averaged in the biomod2 package for R (Thuiller et al., 2019). Models were trained using a random subset of 75% of occurrences, and tested using the remaining 25% of occurrences. We ran 10 training-testing partitions of the occurrence data, and calculated means ± 1 SD of three model performance metrics: Cohen's kappa, the area under the receiver-operator characteristic curve (AUC), and the true skill statistic (TSS; Table S2). We then created an unweighted ensemble average of the five algorithms for each species. We smoothed the results of the ensemble prediction map using a 10 km buffer so that each cell represented the average suitability of cells in a 10 km radius. The resulting raster suitability map for each species had a spatial resolution of 1080 × 1080 m and values ranging from 0 to 1, with 0 indicating unsuitable cells and 1 indicating the most suitable cells.

To define cores for the Rafinesque's big-eared bat and the timber rattlesnake, we selected the 33% of grid cells in the Southeast with highest values in the suitability map to represent the most suitable portions of the landscape for each species. We then removed grid cells that intersected major interstate highways. From the resulting layer of relatively continuous, suitable portions of the landscape, we selected polygons approximately 20 times greater than the mean female home range size determined from the primary literature as cores (Table S1). We selected this size so that mapped cores were big enough to contain several home ranges without being so big as to occupy a large fraction of the study area. To define cores for American black bear models, we modified the approach described above slightly because the most highly-suitable portions of the landscape were almost entirely confined to the state of Florida, and we wanted cores spread throughout suitable habitat across the study area. We therefore selected the 33% of grid cells that had the highest suitability values in each of four quadrants of the study area separately (Fig. S3), intersected those pixels with protected areas in the study region (extracted from the world database of protected areas (UNEP-WCMC and IUCN, 2014)) and selected polygons greater than 20 times the mean female home range size (Table S1).

To identify least-cost linkages between pairs of nodes for each species, we used the inverse of habitat suitability from the ENMs to produce a mapped resistance surface. We input this resistance surface, along with the mapped habitat cores as nodes into Linkage Mapper software (McRae and Kavanagh, 2011). The identification of least-cost paths is one of the most widely-used approaches to connectivity modeling because it is straightforward and intuitive: the route between two nodes that minimizes accumulated resistance across all pixels intersecting the route is the least-cost path for the two nodes. Linkage Mapper calculates linear least-cost linkages within neighborhoods of adjacent nodes by identifying zones around each node. Each zone comprises the pixels closest to a particular node in Euclidian or least-cost space. Nodes are considered adjacent in Linkage Mapper if their zones are juxtaposed, and non-adjacent if it is necessary to pass through an intermediate zone to achieve a connection (McRae and Kavanagh, 2011). We buffered each least-cost linkage by 2.5 km in each direction, for a total width of 5 km, and hereafter these are referred to as the "linkages" for each species. The result was three habitat connectivity networks containing linkages between every habitat core and all adjacent cores based on contemporary landscape and climate conditions.

2.3. Threat from climate change

We defined the threat from climate change for each species in terms of the proportion change in habitat suitability between the contemporary landscape and the landscape in the middle of the 21st century within habitat linkages in the mapped connectivity networks described above. To assess the amount of change expected, we created ENMs for each of the species using projected climate data for the 20-year period centered on 2050 (2041-2060). Future ENMs were based on climate data projections under the IPCC AR4 A2 scenario, which represents a relatively high emissions trajectory (Meehl et al., 2007). We used a consensus approach for projected climate data by gathering projections of future climate from three sources: (1) La Florida (https://floridaclimateinstitute.org/resources/data-sets/regional-downscaling), (2) Eighth-degree CONUS Statistical Asynchronous Regional Regression data (Stoner et al., 2012; available from http://cida.usgs.gov/gdp/), and (3) University of Wisconsin (Tabor and Williams, 2010; available from http://nelson.wisc.edu/ccr/resources/10-minute.php). From each of these sources, we extracted data for three general circulation models (GCMs): CCSM3 (Collins et al., 2006), GFDL CM2.1 (Delworth et al., 2006), and HADCM3 (Pope et al., 2000). We averaged the projected monthly temperature and precipitation across the three GCMs, and calculated projected future values for each of the seven bioclimate variables used for contemporary ENMs. We then projected the ENMs to the 2050 conditions to create an unweighted consensus projection based on future climate. Generally speaking in regional climate projections that span four to five decades like our study, uncertainty among climate models is much larger than scenario uncertainty (Hawkins and Sutton, 2009). Thus, although all future climate data in our study represent only a single emissions scenario, by using an ensemble of nine projected future climates (3 climate models from each of 3 sources of downscaled data), our study design likely captures most of the uncertainty associated with future climate.

To determine climate change threat for each pixel in the study area, we calculated the difference in suitability between each species' contemporary and future ENMs, as a proportion of contemporary suitability. We overlaid the buffered linkages on this suitability change map and calculated the mean change in suitability within each linkage. Linkages for a given species were designated as having a low degree of climate change threat, and thus were designated as refugia, if they were projected to see an increase in suitability, or if the projected decrease in suitability was smaller than the mean decrease across the entire study area. All other linkages had high threat.

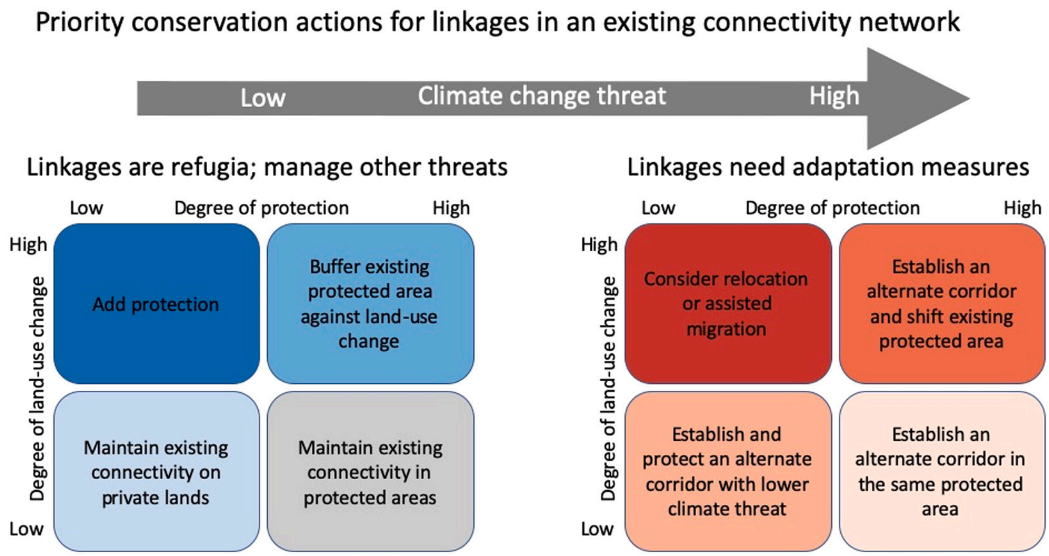

Fig. 1. A typology of example conservation actions for linkages that are of high importance to a connectivity network according to their threat from climate change, degree of projected future land-use change, and degree of protection.

2.4. Defining conservation strategies: combining climate change, land-use change, and protection status for important linkages

To determine priority conservation actions for linkages (research question 4), we developed a relatively simple assessment framework (Fig. 1). Our framework is based on the idea that once the climate threat is known, prioritization of conservation actions on a particular linkage depends on (1) its degree of importance to the overall connectivity network for a species, (2) its non-climate stressors, and (3) its conservation status.

First, the degree of importance of a linkage to the overall network helps determine how critical any conservation action is for maintaining connectivity across the region for each species. Some linkages may be severely degraded by climate change. However, if they are not important to the overall network, losing them may have little influence on species or their populations. Conversely, other linkages may be climate change refugia and central to the overall habitat network; thus, actions on those linkages may be crucial for maintaining connectivity. We identified linkages that were most important to the overall connectivity network for each species using the difference in the Integral Index of Connectivity metric (difference in *IIC*, or *dIIC*, Pascual-Hortal and Saura, 2006). The *IIC* is a measure of habitat availability across a given network that integrates measures of intrapatch and interpatch connectivity, and can be measured for both nodes and linkages. The *IIC* metric thus characterizes the integration of resources across the habitat network, and has been shown to be well-suited for landscape conservation planning (Crouzeilles et al., 2015). We defined important linkages as either: (1) those that were themselves important; that is, those with a *dIIC* in the 90th percentile or above for a given network, or (2) those which connected to at least one of the most important habitat cores in the network – a habitat node with a *dIIC* score in the 90th percentile or above for the network. We used Conefor version 2.6 (Saura and Torné, 2009) for *dIIC* calculations.

The second part of our framework involved a non-climate stressor, land-use change. Because land-use change can fragment habitat, affecting the integrity of the connectivity network, it can be a substantial stressor to consider regardless of the degree of threat from climate change. In the Southeast, expansion of urban land is likely to be one of the most substantial types of land-use change drivers leading to loss of wildlife habitat in the future if recent trends continue (Martinuzzi et al., 2015). To calculate the future degree of land-use change, we used data on projected urbanization for the region (Terando et al., 2014). We created a binary raster of urban/non-urban pixels for the year 2060 by classifying as urban those pixels with at least a 50% probability of urbanization by 2060, and all others as non-urban. Within each buffered important linkage, we calculated the percent change in area of urban land use. We designated linkages as having a high degree of land-use change if their projected change in urban land use was greater than the median for the study area as a whole (139% change; Terando et al., 2014). The geographic extent of the urban projection was slightly smaller than the study area, and did not cover some of the northernmost linkages in Missouri and West Virginia. Those linkages were omitted from this portion of the analysis.

Finally, the range of available management and conservation actions within each linkage will also depend on its protection status; that is, whether it is owned by a public or private agency for conservation or not. We extracted protected areas that are managed for conservation (GAP Status Codes 1, 2, or 3) from the Protected Areas Database (PAD-US) version 1.3 (U.S. Geological Survey Gap Analysis Project, 2012). We calculated the proportion of each buffered important linkage that was under conservation protection. Linkages with a level of protection above the median of 10.0% protected for all land in the study area were designated as having “high protection,” while those at or below the median had “low protection.”

To assess the geographic patterns of priority conservation actions, we overlaid the ecoregion boundaries (U.S. EPA, 2013) on the important linkages. We labeled each ecoregion with the category of protection and threat that corresponded to the largest area of linkages falling within it. For this analysis, we retained only the ecoregions that overlapped at least 100 km^2 of important linkages for a given species.

Except where stated otherwise, analysis here was conducted using ArcGIS 10.1 (Esri, 2012) and R software, version 3.5.3 (R Core Team, 2019) with contributed packages raster (Hijmans, 2016), rgdal (Bivand et al., 2018), and the packages in tidyverse (Wickham, 2017).

3. Results

Mapped linkages for the three focal species, along with *dIIC* metrics, importance status, climate change threat, urbanization threat, and protection status are available at: https://doi.org/10.5061/dryad.z8w9ghx85. The individual and ensemble ecological niche models (ENMs) for each species are available at: https://doi.org/10.5061/dryad.r7sqv9s8v.

The average suitability score for all linkages in the connectivity

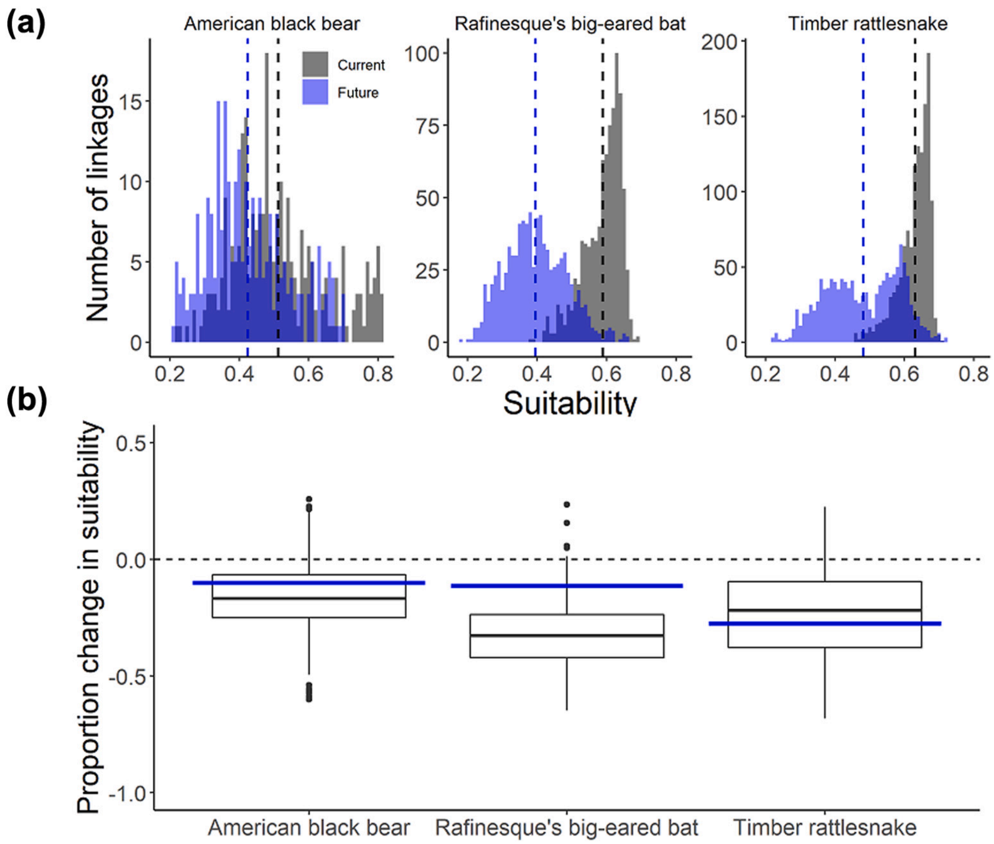

Fig. 2. Modeled suitability results for all mapped linkages for the three species, showing: (a) histograms of suitability for the current and future time periods, and (b) boxplot of proportional change in modeled suitability between the current and future time periods, along with blue lines indicating the average change in suitability for all cells across the landscape (not just within linkages). In (a), bars are slightly transparent, so dark blue indicates overlapping current and future histograms. Dashed lines indicate mean suitability for all linkages for a given species in the current (black) and future (blue) time periods. In (b), boxes represent distribution of values between the first and third quartiles, box centerline shows the median, error bars indicate values no larger than 1.5 times the interquartile range, and dots indicate outliers. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

network of each species decreased in the future (Fig. 2a and b). However, suitability scores of some linkages for each species increased between the current and future time periods.

The three species differed in the degree and geographic pattern of suitability changes. Linkages for the Rafinesque's big-eared bat saw the greatest proportional decline in average suitability among the three species, with an average decrease in suitability of 32.8% (Fig. 2a and b). That decrease was nearly three times greater than the modeled decrease in suitability for the species across the entire study area (not just linkages) (11.3%, blue line in Fig. 2b). As a result, most of the linkages for the bat were classified as having a high degree of threat from climate change. The few linkages that were refugia, showing a low degree of climate change threat, were scattered both in mountain and flatter, low elevation ecoregions (Fig. 3).

In contrast, linkages for the American black bear saw the smallest change in suitability among the three species, with a mean decrease of 15.8% by mid-century (Fig. 2a and b). However, that decrease was greater than the average rate of decrease in suitability for all pixels in the study area for the bear (10.0%). Linkages for the timber rattlesnake saw a moderate decrease in suitability overall (23.4%; Fig. 2a and b), but the snake was the only species for which the average decrease in suitability within linkages was less than that for the region as a whole (27.5%; Fig. 2b). As a result, many linkages for the snake were classified as refugia, having low climate change threat. Those linkages fell in many northern and mountain ecoregions of the study area (Fig. 3).

The snake and bat had similar proportions of all linkages that were among the most important to the overall networks according to our criteria based on *dIIC* (37.4% and 38.4% of linkages for the two species, respectively). A slightly lower proportion of linkages was important for the bear (28.6%). That, combined with the smaller number of linkages overall for the bear, made the set of important linkages for the bear particularly small (74) compared with the bat and snake (341 and 478, respectively).

Among the three species, the Rafinesque's big-eared bat had the largest proportion of important linkages with high threat from climate change, and thus the largest proportion in need of adaptation measures (Figs. 4 and 5). Almost half of important linkages for the bat (46.0%) had high climate change threat, high land-use change threat, and low degree of protection, suggesting that ex-situ conservation actions should be a priority. An additional one-third (32.8%) had high climate change threat, low land-use change threat, and low protection (Fig. 4). Linkages with high climate threat and little protection were the predominant threat-protection categories for the bat in all but two ecoregions (Fig. 6).

Like Rafinesque's big-eared bat, most of the important linkages for the American black bear had high levels of threat from climate change and a low degree of protection (Fig. 4). Nearly one-third (31.1%) of important linkages had high climate change threat, low land-use change threat, and a low degree of protection, suggesting that protecting an alternative corridor should be considered a priority. An additional one quarter (25.7%) of important linkages had high degrees of both climate change and land-use change threat with a low degree of protection. However, compared with the bat, a higher proportion of important linkages (8.1%), and thus a higher number of ecoregions, had low degrees of climate change threat combined with higher than average protection (Figs. 4 and 5). Ecoregions with low climate change threat were located in both the high-elevation northern ecoregion and the low-elevation western and southwestern ecoregions (Fig. 6).

In contrast, the timber rattlesnake was the only species for which the majority of important linkages had low threat from climate change (Figs. 4 and 5). Within the low climate threat category, the largest proportion (20.7%) of the snake's important linkages had high land-use threat and low protection status, suggesting that adding protection should be a priority. However, important linkages with low degrees of both threats, whether with low (16.5%) or high (14.9%) degrees of protection, were also relatively common for the snake. Linkages with lower climate change threat occurred across many northern and mountains ecoregions (Fig. 6).

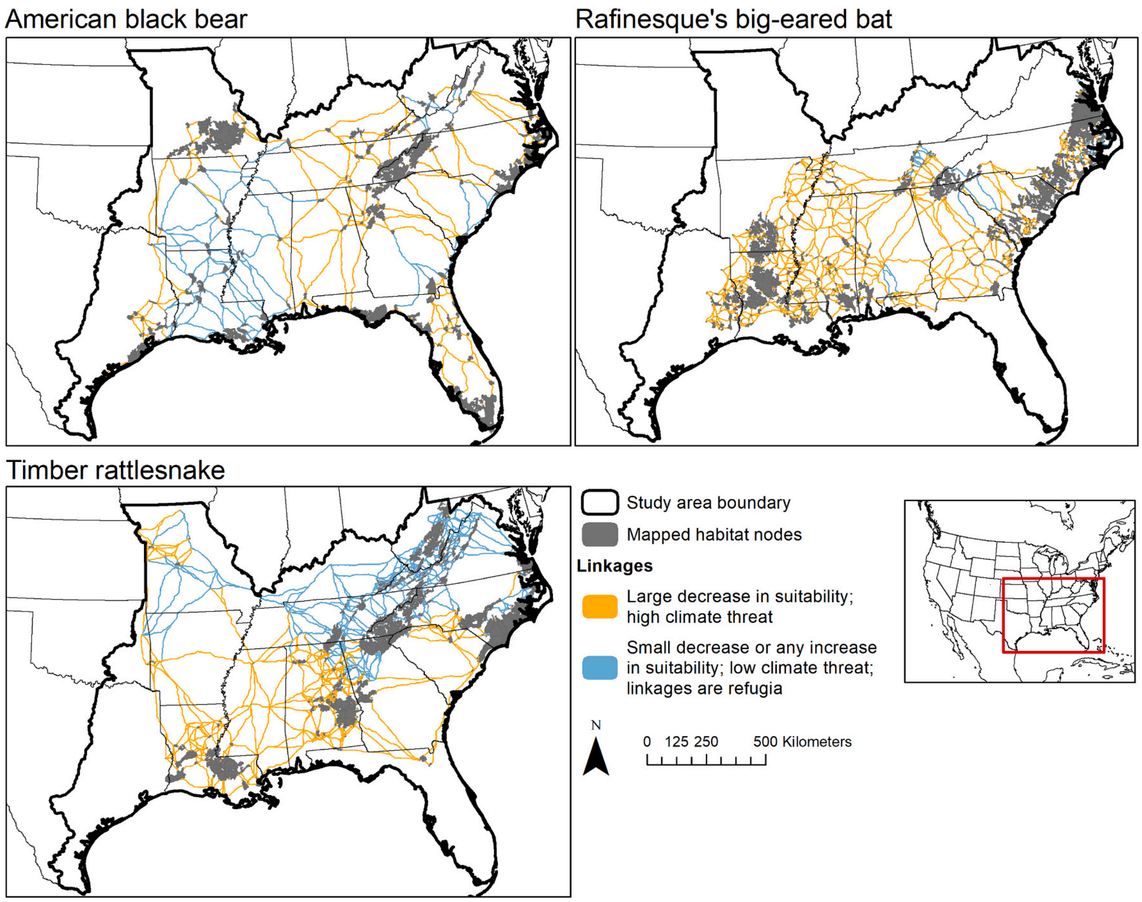

Fig. 3. Mapped connectivity networks for all species, showing habitat nodes and linkages. Linkages are colored according to their change in modeled habitat suitability due to climate change between current and future time periods, and those with low climate threat are considered to be refugia. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

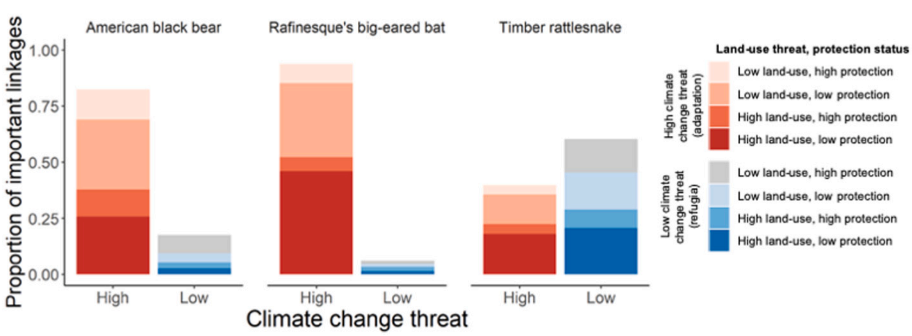

Fig. 4. Proportions of each species' important linkages characterized by category of climate change threat, land-use change threat, and degree of protection. Colors match Fig. 1 and thus represent the distribution of suggested conservation actions for each species' linkages. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

All three focal species differed in the degree to which climate change threatens connectivity, the geography of that threat and others, and therefore the priority conservation strategies required for maintaining connectivity under climate change. This means that, despite all species using similar habitat in the Southeastern U.S., there is no one-size-fits-all for connectivity conservation as climate and land use change. In our example, climate adaptation strategies will be critical for habitat linkages for Rafinesque's big-eared bats and American black bears, while managing non-climate threats such as land-use change will be a priority for timber rattlesnakes.

Our results inform priority actions for conserving habitat connectivity under climate change, with these three focal species likely acting as representatives for many other similar species. For species like the snake that have linkages that are climate-stable relative to the landscape as a whole, managing the non-climate stressors will be critical. According to our framework, because many of the snake's linkages had low rates of protection paired with either low or high rates of land-use change, adding protection within and buffering existing protected areas against land-use change are both priorities for the species.

For species like the bat and bear, whose linkages are highly threatened by climate change relative to the surrounding landscape, identifying strategies for adaptation are priorities. The high degree of threat from climate change for these species is exacerbated because linkages tended to have a low degree of protection, and many had a high degree of urbanization. This result suggests that ex-situ conservation strategies like managed relocation or assisted migration to sites that already have high protection (Fig. 1, also see Oliver et al., 2012) could be critical. Finding and protecting an alternative linkage in an area adjacent to an

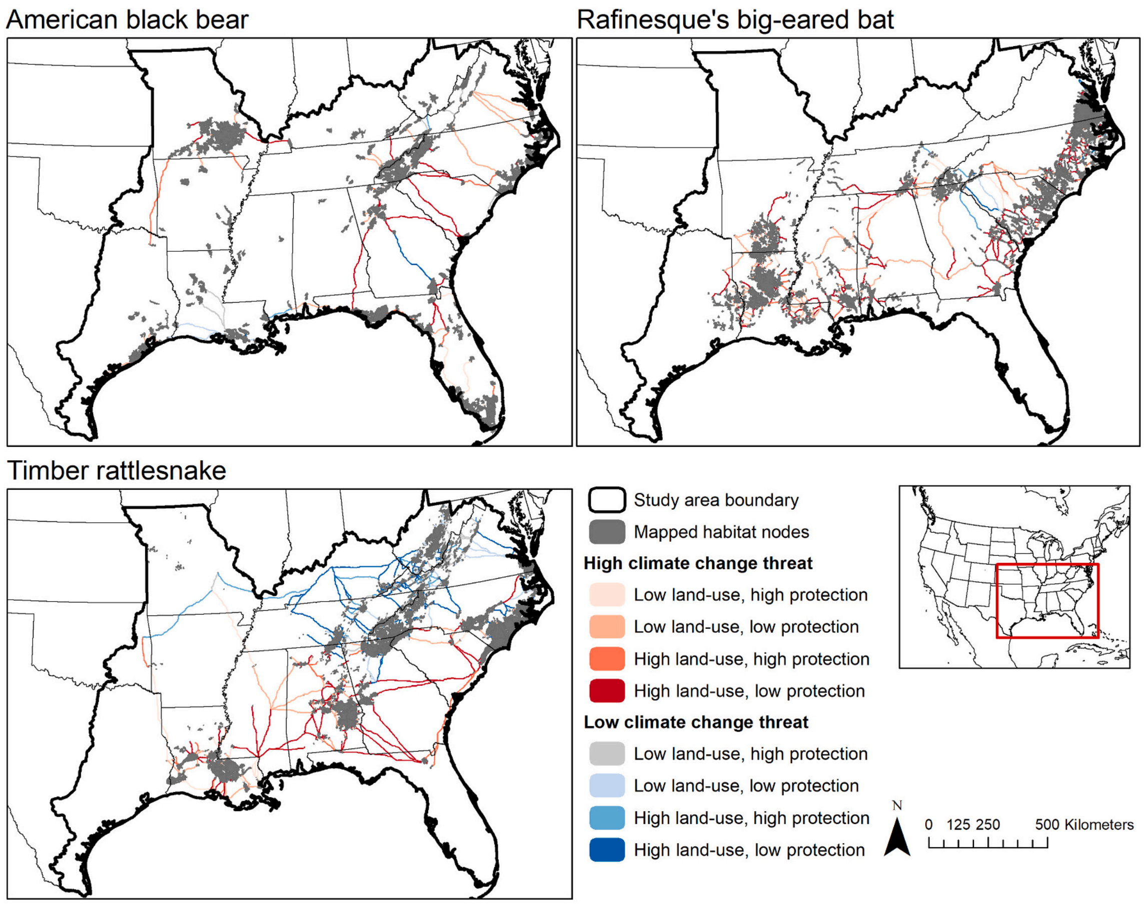

Fig. 5. Maps of each species' important linkages in each of the eight categories of climate change threat, land-use change, and degree of protection. Colors match Fig. 1 and thus represent the suggested conservation actions for each linkage. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

existing linkage that has a lower climate threat is another priority action, especially for some linkages in which urban growth is not likely to be as rapid. Alternate linkages that have lower degrees of climate change threat could be readily identifiable for these species, since the surrounding landscapes for those species had relatively low climate threat. In addition, one notable difference between the bat and bear is that the bear is able to disperse longer distances and can use human-dominated habitats (Evans et al., 2017; Lee and Vaughan, 2003). Thus, identifying and protecting alternative linkages may be met with more success for the bear than for the bat, which is more limited by dispersal and habitat.

Variation in life history and geographic distributions likely explains many of the differences among species in our results. The geographic range of the timber rattlesnake in the Southeast is known to be sensitive to climate (Lawing and Polly, 2011), and is more sensitive than the ranges of the other two species. This likely explains why the average decrease in suitability across the landscape as a whole (but not for linkages) for the snake was greater than for the other two species. However, the snake was the only species for which the most important existing linkages were also more climate-stable in the future scenario relative to the landscape as a whole. We suggest this is because many of the linkages that were most important to the connectivity network for the species were located in higher elevations, due to the high concentration of all habitat cores and linkages there. As such, the snake followed expected patterns for a species whose range is climate-sensitive; i.e. lower climate change threat and more climate change refugia in the northern and mountainous regions, and more threat from climate change in other regions.

In contrast to the timber rattlesnake, the American black bear and Rafinesque's big-eared bat are more habitat generalist species and are found in a range of climates in the Southeast. That could explain why, for the bear, linkages and the study area as a whole saw the smallest decreases in suitability. Linkages that retained their suitability better than the surrounding landscape (linkages with low climate threat in Fig. 3) were largely in the low-elevation and southern portions of the study area. And, like the bear, the bat's range as a whole in the Southeast is not as climate-restricted as the timber rattlesnake's. Thus, the decrease in suitability across the landscape for the bat was almost as small as the bear. However, unlike the bear, nearly all linkages for the bat had high climate threat relative to the rest of the landscape, and the few linkages that had low climate threat were relatively scattered across the study area with no overall discernable geographic pattern.

Urbanization is likely to be a substantial threat to all three species. It has been a dominant type of land-use change recently in the region (Wear and Greis, 2013), and is expected to be substantial across the study area by mid-century (Terando et al., 2014). Thus, for all species, it is imperative to act soon in order to increase protection in linkages and prevent the effects of impending development before it occurs. Many of the habitats in the Southeast are increasingly under a number of other pressures that are critical to incorporate into conservation planning. These include the effects of salt water intrusion from sea-level rise and storm surges (Bhattachan et al., 2018), increased woody biomass harvest to meet global wood pellet demand (Costanza et al., 2017), and increased demand for agricultural crops (Martinuzzi et al., 2015). For example, Leonard et al. (2016) showed that, for a set of species including the American black bear and timber rattlesnake, sea-level rise is expected to have larger effects than urbanization on connectivity in some coastal ecoregions within our study area.

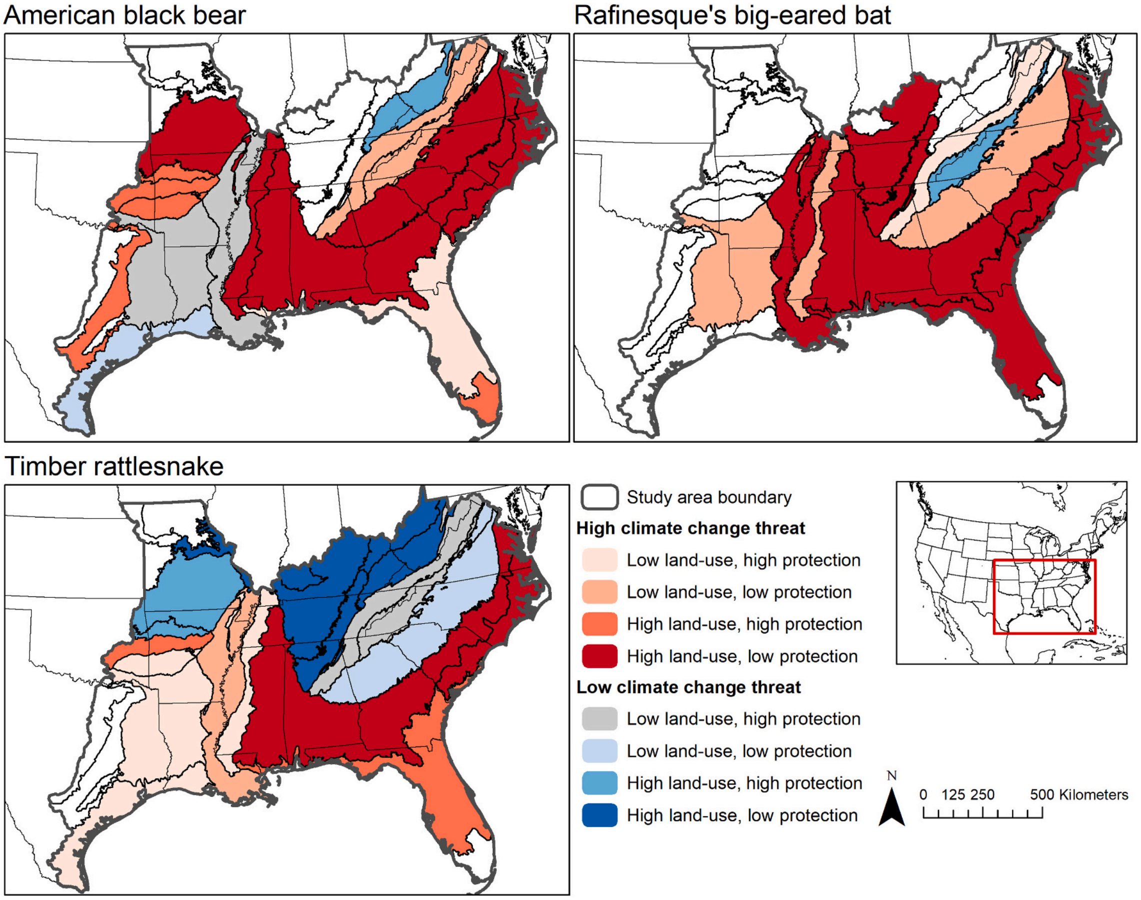

Fig. 6. Predominant threat-protection category for important linkages by ecoregion. Ecoregions shown but not filled for a given species in were excluded because they contained little or none of the important linkages for the species. Colors match Fig. 1 and thus represent the major suggested conservation actions for linkages within each ecoregion. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The broad extent of our study allowed us to evaluate threats and identify actions for conservation of multiple focal species at a scale relevant to regional policy and planning. However, that extent, along with the relatively coarse resolution of our input data and modeling approach also influenced our results. Because of the resolution of available climate data across the regional domain, the ENMs and buffered linkages have relatively coarse spatial resolutions (1 km^2 pixels for the ENMs and 5 km buffers around linkages). While broad corridors may be desirable under climate change to ensure a variety of habitats no matter the focal species (Keeley et al., 2018), the coarse scale of our study meant that we likely missed finer-scale patterns of climate change threat and local refugia. Such fine-scale refugia likely exist especially for timber rattlesnakes and Rafinesque's big-eared bats, given their relatively small home range sizes (< < 5 km^2). Thus, an important next step for conservation of those species will be to conduct similar studies at smaller extents to identify local refugia and determine specific actions that should be taken on individual land parcels. For such studies and for climate change connectivity research more generally, it will be critical for climate scientists and ecologists to co-produce climate and other physiographic data, at least for localized areas, at resolutions relevant for wildlife species that sample their environments at fine scales.

By assessing the threats to connectivity for multiple focal species, we examined the range of possible future outcomes in the region. We used five ENM algorithms, and three sets of downscaled climate projections for each of three global climate models per species in order to overcome warnings that species-based approaches can lead to overly precise conservation priorities (Kujala et al., 2013a,b). One way we could build on this approach is by producing an ensemble of connectivity networks, one for each combination of ENM, climate projection and climate model, for each species to more fully capture the range of uncertainty for conservation planning (Meller et al., 2014). Relatedly, by developing ENMs for future climate that extrapolate observed correlations between species occurrences, climate, and existing vegetation, we are likely failing to capture all of the complex ways in which climate change could affect these species, their population dynamics, and other aspects of their life history. For example, warmer temperature causes earlier den emergence for American black bears (Miller et al., 2017). Thus, climate change could lead to decreased hibernation and additional human-wildlife conflict for that species, especially as human populations increase and urban land use expands, and we were unable to consider that here.

Despite the substantial threats faced by these species and their habitat networks under global change, the prospect of connectivity conservation does show some promise in the Southeast and beyond. For example, in the Southeast, the Southeast Conservation Adaptation Strategy (SECAS; http://secassoutheast.org/) is a multi-entity partnership whose conservation goals include increased connectivity in the region by 2060. Elsewhere, large connectivity plans are being developed for large groups of species across entire countries (for example, Choe et al., 2017). On a global level, the United Nations Environment Programme (UNEP) recently identified ecological connectivity as a key emerging issue for biodiversity conservation (UNEP, 2019). We are thus optimistic that connectivity conservation will be prioritized, and that existing networks will play an important role in ensuring species' survival in the future.

5. Conclusions

Existing connectivity networks face extensive threats from climate and land-use change. By examining the degree and geographic patterns of these threats to connectivity for a set of focal species, our research suggests that not all species will fare the same when it comes to conserving existing connectivity under climate change, and that priority actions may vary by individual species. We found that existing linkages for the more specialist species whose range is restricted by climate were more likely to serve as climate change refugia, as compared to linkages for the more generalist species. And, geographic patterns of climate threat to connectivity for the range-restricted species tended to more closely follow regional climate gradients, with climate threat higher in the southern latitudes and in flatter, high climate velocity areas. We suspect similar results will be seen for other generalist versus range-restricted species, and further work will be required to determine for which species, and under which circumstances, the patterns will hold. Despite the serious threats to the habitats of these species, we are hopeful that conservation of existing connectivity can be achieved, and we have aimed to provide critical information toward that goal. However, in all cases, and especially for species or for linkages with relatively high threats from land-use change, acting relatively quickly, before these projected changes occur, will be key to ensuring the success of conservation efforts.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108678.

CRediT authorship contribution statement

Jennifer K. Costanza:Conceptualization, Methodology, Formal analysis, Visualization, Writing - original draft, Writing - review & editing.**James Watling**:Conceptualization, Methodology, Software, Writing - original draft, Writing - review & editing.**Ron Sutherland**: Conceptualization, Methodology, Software, Writing - review & editing.**Curtis Belyea**:Software.**Bistra Dilkina**:Conceptualization. **Heather Cayton**:Writing - review & editing.**David Bucklin**: Software.**Stephanie Romañach**:Conceptualization, Writing - review & editing, Funding acquisition.**Nick M. Haddad**:Conceptualization, Writing - review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank J. Guzy and two anonymous reviewers for insightful comments that greatly improved this manuscript. This research was funded by the Department of the Interior Southeast Climate Adaptation Science Center. The project described in this publication was supported by Cooperative Agreement Nos. G12AC20503 and G16AP00129 from the United States Geological Survey. This manuscript is submitted for publication with the understanding that the United States Government is authorized to reproduce and distribute reprints for Governmental purposes. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Bayless, M.L., Clark, M.K., Stark, R.C., Douglas, B.S., Ginger, S.M., 2011. Distribution and status of eastern big-eared bats (Corynorhinus spp.)., pp. 13–25, in: Loeb, S.C., Lacki, M.J., Miller, D.A. (Eds.), Conservation and Management of Eastern Big-Eared Bats: A Symposium. USDA Forest Service General Technical Report SRS-145., Asheville, NC, USA. 157 pages.

Bhattachan, A., Emanuel, R.E., Ardon, M., Bernhardt, E.S., Anderson, S.M., Stillwagon, M.G., Ury, E.A., BenDor, T.K., Wright, J.P., 2018. Evaluating the effects of land-use change and future climate change on vulnerability of coastal landscapes to saltwater intrusion. Elem. Sci. Anth. 62, 1–11. https://doi.org/10.1525/elementa.316.

Bivand, R., Keitt, T., Rowlingson, B., 2018. rgdal: bindings for the "geospatial" data abstraction library. R package version 1.3-4. https://CRAN.R-project.org/package=rgdal.

Breiman, L., 2001. Random forests. Mach. Learn. 45, 5–32. https://doi.org/10.1023/A:1010933404324.

Choe, H., Thorne, J.H., Hijmans, R., Kim, J., Kwon, H., Seo, C., 2017. Meta-corridor solutions for climate-vulnerable plant species groups in South Korea. J. Appl. Ecol. 54, 1742–1754. https://doi.org/10.1111/1365-2664.12865.

Clark, R.W., Brown, W.S., Stechert, R., Zamudio, K.R., 2010. Roads, interrupted dispersal, and genetic diversity in timber rattlesnakes. Conserv. Biol. 24, 1059–1069. https://doi.org/10.1111/j.1523-1739.2009.01439.x.

Collins, W.D., Bitz, C.M., Blackmon, M.L., Bonan, G.B., Bretherton, C.S., Carton, J.A., Chang, P., Doney, S.C., Hack, J.J., Henderson, T.B., Kiehl, J.T., Large, W.G., McKenna, D.S., Santer, B.D., Smith, R.D., 2006. The community climate system model version 3 (CCSM3). J. Clim. 19, 2122–2143. https://doi.org/10.1175/JCLI3761.1.

Costanza, J.K., Terando, A.J., 2019. Landscape connectivity planning for adaptation to future climate and land-use change. In: Curr. Landsc. Ecol. Reports, https://doi.org/10.1007/s40823-019-0035-2.

Costanza, J.K., Abt, R.C., McKerrow, A.J., Collazo, J.A., 2017. Bioenergy production and forest landscape change in the southeastern United States. GCB Bioenergy 9, 924–939. https://doi.org/10.1111/gcbb.12386.

Crouzeilles, R., Beyer, H.L., Mills, M., Grelle, C.E.V., Possingham, H.P., 2015. Incorporating habitat availability into systematic planning for restoration: a species-specific approach for Atlantic Forest mammals. Divers. Distrib. 21, 1027–1037. https://doi.org/10.1111/ddi.12349.

Delworth, T.L., Broccoli, A.J., Rosati, A., Stouffer, R.J., Balaji, V., Beesley, J.A., Cooke, W., Dixon, K.W., Dunne, J., Dunne, K.A., Durachta, J.W., Findell, K.L., Ginoux, P., Gnanadesikan, A., Gordon, C.T., Griffies, S.M., Gudgel, R., Harrison, M.J., Held, I., Hemler, R.S., Horowitz, L.W., Klein, S.A., Knutson, T.R., Kushner, P.J., Langenhorst, A.R., Lee, H.-C., Lin, S.-J., Lu, J., Malyshev, S.L., Milly, P.C.D., Ramaswamy, V., Russell, J., Schwarzkopf, M.D., Shevliakova, E., Sirutis, J.J., Spelman, M.J., Stern, W.F., Winton, M., Wittenberg, A.T., Wyman, B., Zeng, F., Zhang, R., 2006. GFDL's CM2 global coupled climate models. Part I: formulation and simulation characteristics. J. Clim. 19, 643–674.

Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77, 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x.

Environmental Protection Agency (EPA), 2004. Level III and IV Ecoregions of EPA Region 4. U.S. Environmental Protection Agency, National Health and Environmental Effects Research Laboratory, Western Ecology Division, Corvallis, OR, USA.

Esri, 2012. ArcGIS Desktop: Release 10.1.

Evans, M.J., Rittenhouse, T.A.G., Hawley, J.E., Rego, P.W., 2017. Black bear recolonization patterns in a human-dominated landscape vary based on housing: new insights from spatially explicit density models. Landsc. Urban Plan. 162, 13–24. https://doi.org/10.1016/j.landurbplan.2017.01.009.

Friedman, J.H., 1991. Multivariate adaptive regression splines. Ann. Stat. 19, 1–67.

Hällfors, M.H., Aikio, S., Schulman, L.E., 2017. Quantifying the need and potential of assisted migration. Biol. Conserv. 205, 34–41. https://doi.org/10.1016/j.biocon.2016.11.023.

Hao, T., Elith, J., Guillera-Arroita, G., Lahoz-Monfort, J.J., 2019. A review of evidence about use and performance of species distribution modelling ensembles like BIOMOD. Divers. Distrib. 25, 839–852. https://doi.org/10.1111/ddi.12892.

Hawkins, E., Sutton, R., 2009. The potential to narrow uncertainty in regional climate predictions. Bull. Am. Meteorol. Soc. 90, 1095–1107. https://doi.org/10.1175/2009BAMS2607.1.

Heller, N.E., Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biol. Conserv. 142, 14–32. https://doi.org/10.1016/j.biocon.2008.10.006.

Hijmans, R.J., 2016. raster: geographic data analysis and modeling. R package version 2.5-8. https://CRAN.R-project.org/package=raster.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Johnson, J.S., 2012. Foraging and Roosting Behaviors of Rafinesque's Big-eared Bat (*Corynorhinus rafinesquii*) as the Northern Edge of the Species' Range. University of Kentucky.

Johnson, J.S., Lacki, M.J., 2013. Habitat associations of Rafinesque's big-eared bats (Corynorhinus rafinesquii) and their lepidopteran prey in bottomland hardwood forests. Can. J. Zool. 91, 94–101. https://doi.org/10.1139/cjz-2012-0248.

Johnson, J.S., Kropczynski, J.N., Lacki, M.J., Langlois, G.D., 2012. Social networks of Rafinesque's big-eared bats (Corynorhinus rafinesquii) in bottomland hardwood forests. J. Mammal. 93, 1545–1558. https://doi.org/10.1644/12-mamm-a-097.1.

Keeley, A.T.H., Ackerly, D.D., Cameron, D.R., Heller, N.E., Huber, P.R., Schloss, C.A., Thorne, J.H., Merenlender, A.M., 2018. New concepts, models, and assessments of climate-wise connectivity. Environ. Res. Lett. 13, 073002. https://doi.org/10.1088/1748-9326/aacb85.

Keppel, G., Van Niel, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., Schut, A.G.T., Hopper, S.D., Franklin, S.E., 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. Glob. Ecol. Biogeogr. 21, 393–404. https://doi.org/10.1111/j.1466-8238.2011.00686.x.

Kujala, H., Burgman, M.A., Moilanen, A., 2013a. Treatment of uncertainty in

conservation under climate change. Conserv. Lett. 6, 73–85. https://doi.org/10.1111/j.1755-263X.2012.00299.x.
Kujala, H., Moilanen, A., Araújo, M.B., Cabeza, M., 2013b. Conservation planning with uncertain climate change projections. PLoS One 8. https://doi.org/10.1371/journal.pone.0053315.
Larkin, J.L., Maehr, D.S., Hoctor, T.S., Orlando, M.A., Whitney, K., 2004. Landscape linkages and conservation planning for the black bear in west-central Florida. Anim. Conserv. 7, 23–34. https://doi.org/10.1017/S1367943003001100.
Lawing, A.M., Polly, P.D., 2011. Pleistocene climate, phylogeny, and climate envelope models: an integrative approach to better understand species' response to climate change. PLoS One 6. https://doi.org/10.1371/journal.pone.0028554.
Lawler, J.J., Ruesch, A.S., Olden, J.D., McRae, B.H., 2013. Projected climate-driven faunal movement routes. Ecol. Lett. 16, 1014–1022. https://doi.org/10.1111/ele.12132.
Lee, D.J., Vaughan, M.R., 2003. Dispersal movements by subadult American black bears in Virginia. Ursus 14, 162–170. https://doi.org/10.2307/3873016.
Leonard, P.B., Sutherland, R.W., Baldwin, R.F., Fedak, D.A., Carnes, R.G., Montgomery, A.P., 2016. Landscape connectivity losses due to sea level rise and land use change. Anim. Conserv. https://doi.org/10.1111/acv.12289.
Littlefield, C.E., Krosby, M., Michalak, J.L., Lawler, J.J., 2019. Connectivity for species on the move: supporting climate-driven range shifts. Front. Ecol. Environ. https://doi.org/10.1002/fee.2043. fee. 2043.
Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B., Ackerly, D.D., 2009. The velocity of climate change. Nature 462, 1052–1055. https://doi.org/10.1038/nature08649.
Mantyka-Pringle, C.S., Martin, T.G., Rhodes, J.R., 2012. Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. Glob. Chang. Biol. 18, 1239–1252. https://doi.org/10.1111/j.1365-2486.2011.02593.x.
Mantyka-Pringle, C.S., Martin, T.G., Moffatt, D.B., Udy, J., Olley, J., Saxton, N., Sheldon, F., Bunn, S.E., Rhodes, J.R., 2016. Prioritizing management actions for the conservation of freshwater biodiversity under changing climate and land-cover. Biol. Conserv. 197, 80–89. https://doi.org/10.1016/j.biocon.2016.02.033.
Martinuzzi, S., Withey, J.C., Pidgeon, A.M., Plantinga, A.J., McKerrow, A.J., Williams, S.G., Helmers, D.P., Radeloff, V.C., 2015. Future land-use scenarios and the loss of wildlife habitats in the southeastern United States. Ecol. Appl. 25, 160–171. https://doi.org/10.1890/13-2078.1.
McCullagh, P., 1984. Generalized linear models. Eur. J. Oper. Res. 16, 285–292.
McGuire, J.L., Lawler, J.J., McRae, B.H., Nuñez, T.A., Theobald, D.M., 2016. Achieving climate connectivity in a fragmented landscape. Proc. Natl. Acad. Sci. 113, 7195–7200. https://doi.org/10.1073/pnas.1602817113.
McLachlan, J.S., Hellmann, J.J., Schwartz, M.W., 2007. A framework for debate of assisted migration in an era of climate change. Conserv. Biol. 21, 297–302. https://doi.org/10.1111/j.1523-1739.2007.00676.x.
McRae, B., Kavanagh, D., 2011. Linkage Mapper Connectivity Analysis Software, Seattle, Washington, USA.
Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J., Zhao, Z.-C., 2007. Global climate projections. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, U.K., and New York, NY, USA.
Meller, L., Cabeza, M., Pironon, S., Barbet-Massin, M., Maiorano, L., Georges, D., Thuiller, W., 2014. Ensemble distribution models in conservation prioritization: from consensus predictions to consensus reserve networks. Divers. Distrib. 20, 309–321. https://doi.org/10.1111/ddi.12162.
Miller, J.A., Smith, T.S., Auger, J., Black, H.L., Allphin, L., 2017. The late-denning activities of the American black bear in Utah. Ursus 27, 78–89. https://doi.org/10.2192/ursu-d-15-00035.1.
Morelli, T.L., Daly, C., Dobrowski, S.Z., Dulen, D.M., Ebersole, J.L., Jackson, S.T., Lundquist, J.D., Millar, C.I., Maher, S.P., Monahan, W.B., Nydick, K.R., Redmond, K.T., Sawyer, S.C., Stock, S., Beissinger, S.R., 2016. Managing climate change refugia for climate adaptation. PLoS One 11, 1–17. https://doi.org/10.1371/journal.pone.0159909.
NatureServe, 2019b. NatureServe Explorer: an online encyclopedia of life [web application]. Version 7.0. NatureServe, Arlington, VA, U.S.A. [WWW Document]. URL http://explorer.natureserve.org/ (accessed 3.1.19).
Nuñez, T.A., Lawler, J.J., McRae, B.H., Pierce, D.J., Krosby, M.B., Kavanagh, D.M., Singleton, P.H., Tewksbury, J.J., 2013. Connectivity planning to address climate change. Conserv. Biol. 27, 407–416. https://doi.org/10.1111/cobi.12014.
Oliver, T.H., Smithers, R.J., Bailey, S., Walmsley, C.A., Watts, K., 2012. A decision framework for considering climate change adaptation in biodiversity conservation planning. J. Appl. Ecol. 49, 1247–1255. https://doi.org/10.1111/1365-2664.12003.
Pascual-Hortal, L., Saura, S., 2006. Comparison and development of new graph-based landscape connectivity indices: towards the priorization of habitat patches and corridors for conservation. Landsc. Ecol. 21, 959–967. https://doi.org/10.1007/s10980-006-0013-z.
Peterson, A.T., Soberon, J., Pearson, R.G., Anderson, R.P., Martinez-Meyer, E., Nakamura, M., Araújo, M., 2011. Ecological Niches and Geographic Distributions. Princeton University Press, Princeton, New Jersey, USA.
Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026.
Pope, V.D., Gallani, M.L., Rowntree, P.R., Stratton, R.A., 2000. The impact of new physical parametrizations in the Hadley Centre climate model: HadAM3. Clim. Dyn. 16, 123–146. https://doi.org/10.1007/s003820050009.
R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Rudnick, D.A., Ryan, S.J., Beier, P., Cushman, S.A., Dieffenbach, F., Epps, C.W., Gerber, L.R., Hartter, J., Jenness, J.S., Kintsch, J., Merenlender, A.M., Perkl, R.M., Preziosi, D.V., Trombulak, S.C., 2012. The role of landscape connectivity in planning and implementing conservation and restoration priorities. In: Issues Ecol, pp. 16.
Saura, S., Torné, J., 2009. Conefor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity. Environ. Model. Softw. 24, 135–139. https://doi.org/10.1016/j.envsoft.2008.05.005.
Steen, D.A., Smith, L.L., Conner, L.M., Brock, J.C., Hoss, S.K., 2007. Habitat use of sympatric rattlesnake species within the Gulf Coastal Plain. J. Wildl. Manag. 71, 759–764. https://doi.org/10.2193/2005-754.
Stoner, A.M.K., Hayhoe, K., Yang, X., Wuebbles, D.J., 2012. An asynchronous regional regression model for statistical downscaling of daily climate variables. Int. J. Climatol. 33, 2473–2494. https://doi.org/10.1002/joc.3603.
Stratman, M.R., Alden, D.C., Pelton, M.R., Sunquist, M.E., Alden, C.D., 2001. Habitat use by American black bears in the sandhills of Florida. Ursus 12, 109–114.
Tabor, K., Williams, J., 2010. Globally downscaled climate projections for assessing the conservation impacts of climate change. Ecol. Appl. 20, 554–565. https://doi.org/10.1890/09-0173.1.
Terando, A., Costanza, J.K., Belyea, C., Dunn, R.R., McKerrow, A.J., Collazo, J.A., 2014. The southern megalopolis: using the past to predict the future of urban sprawl in the Southeast U.S. PLoS One 9, e102261.
Thuiller, W., Georges, D., Engler, R., Breiner, F., 2019. biomod2: ensemble platform for species distribution modeling. Available at: https://CRAN.R-project.org/package=biomod2.
U.S. Environmental Protection Agency (U.S. EPA), 2013. Level III and IV Ecoregions of the Continental United States. Corvallis, OR, USA. Available at. http://www.epa.gov/wed/pages/ecoregions/level_iii_iv.htm, Accessed date: August 2013.
U.S. Geological Survey Gap Analysis Project, 2012. Protected areas database-US (PAD-US), version 1.3. Available at. http://gapanalysis.usgs.gov/padus/, Accessed date: July 2013.
UNEP, 2019. Frontiers 2018/19 Emerging Issues of Environmental Concern, United Nations Environment Programme. Nairobi, Kenya. https://doi.org/978-92-807-3553-6.
UNEP-WCMC, IUCN, 2014. Protected Planet: The World Database on Protected Areas (WDPA)/The Global Database on Protected Areas Management Effectiveness (GD-PAME) [online]. UNEP-WCMC and IUCN, Cambridge, UK Available at. www.protectedplanet.net, Accessed date: June 2014.
USGCRP, 2017. Climate Science Special Report: Fourth National Climate Assessment, Volume I.
Waldron, J.L., Bennett, S.H., Welch, S.M., Dorcas, M.E., Lanham, J.D., Kalinowsky, W., 2006a. Habitat specificity and home-range size as attributes of species vulnerability to extinction: a case study using sympatric rattlesnakes. Anim. Conserv. 9, 414–420. https://doi.org/10.1111/j.1469-1795.2006.00050.x.
Waldron, J.L., Lanham, J.D., Bennett, S.H., 2006b. Using behaviorally-based seasons to investigate canebrake rattlesnake (Crotalus horridus) movement patterns and habitat selection. Herpetologica 62, 389–398. https://doi.org/10.1655/0018-0831(2006)62[389:ubstic]2.0.co;2.
Wear, D.N., Greis, J.G., 2013. The southern forest futures project: technical report., USDA Forest Service Gen. Tech. Rep. SRS-178. Asheville, NC, USA. 542 pages.
Wickham, H., 2017. Tidyverse: easily install and load "tidyverse" packages. R package version 1.1.1.
Wickham, J., Homer, C., Vogelmann, J., McKerrow, A., Mueller, R., Herold, N., Coulston, J., 2014. The multi-resolution land characteristics (MRLC) consortium - 20 years of development and integration of USA national land cover data. Remote Sens. 6, 7424–7441. https://doi.org/10.3390/rs6087424.